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WEB CONSTRUCTION BY *MODISIMUS* SP. (ARANEAE, PHOLCIDAE)

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ABSTRACT. The behavior used by *Modisimus* sp. to construct its domed sheet web is more stereotyped and organized than is apparent from the finished structure. A simple program involving attaching the non-sticky dragline to the substrate beyond the previous limits of the web, and then filling in the newly formed angle is probably used to construct the skeleton sheet and the tangle above it. A set of sticky lines is then laid, filling in this sheet. Construction behavior resembles that of orb weavers in commencing with a skeleton scaffold of non-sticky lines which is then filled in with other non-sticky lines, in adding sticky lines after the support structure of non-sticky lines is complete, and in being organized around a central area.

It is commonly stated in general texts that pholcid spiders make non-adhesive tangle webs with little or no organization (e.g., Levi, Levi & Zim 1968; Forster & Forster 1973; Foelix 1982; Shinkai 1984; Shear 1986). Most accounts are apparently based primarily on the webs of the temperate species *Pholcus phalangiodes* (Fuesslin). With the slow accumulation of data on tropical pholcids, it is becoming clear that there is a rich diversity of web forms in this family (Eberhard & Briceño 1985; Deeleman-Reinhold 1986; Eberhard in press a on *Physocyclus globosus* Taczanowski), and that some pholcid webs include sticky lines (Briceño 1985), and entangling "screw threads" (Kirchner 1986).

Other than the mention of two stages of web construction in two *Modisimus* spp. (Eberhard & Briceño 1985), there are, to my knowledge, no descriptions of how pholcid webs are built (or, for that matter, of the construction of almost any other non-orb web; Eberhard 1990a). Given the relatively isolated taxonomic position of Pholcidae (e.g., Lehtinen 1967; Shear 1986), the means by which they produce aerial sheet webs with sticky lines are likely to prove of interest in comparison with construction of webs in other families. This paper describes the construction of such webs by a third *Modisimus* species.

METHODS

Spiders were observed during daylight hours on 22–25 February, 1991 on fallen trees and buttresses in an overgrown cocoa orchard at La Selva Biological Station, near Puerto Viejo, Heredia Province, Costa Rica (el. about 50 m). At least part of the construction of 21 different webs was observed. Web construction was elicited by partially or nearly completely destroying the web on which the spider was found. Some webs were coated with cornstarch before being destroyed. I included observations of spiders that started to build replacement webs 5–45 min after their webs were destroyed.

Several partially completed webs were coated with cornstarch. By recoating these webs lightly when they were finished, it was possible to distinguish the order in which lines had been laid (more heavily coated lines first, others later). The stages of construction behavior in partial and complete web replacement were similar, and the two are combined in the descriptions below.

Samples of adult webs, collected by wetting the edges of a microscope slide and then lifting it through the web, were viewed at 400× with direct illumination.

Spiders were identified by C. Deeleman-Reinhold. The species, which seems close to *M. pulchellus* Banks 1929, is apparently undescribed. Voucher specimens are deposited in the Museum of Comparative Zoology, Cambridge, MA 02138 (Nos. 3604, 3606, 3611), and in the collection of C. Deeleman-Reinhold (Sparrenlaan 8, Ossendrecht, The Netherlands). This species is different from the *Modisimus* species whose behavior was described previously (Eberhard & Briceño 1983, 1985).

RESULTS

Finished webs.—Webs of *Modisimus* sp. were found attached to large supporting objects such as the buttresses of trees or fallen logs (Fig. 1). Web sites were usually sheltered from at least

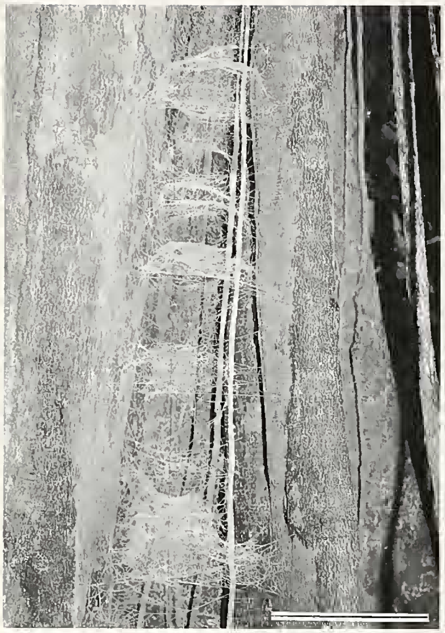


Figure 1.—Webs of *Modisimus* sp. on the heavily populated base of a tree trunk with deep indentations. Note the variability in web design. Scale bar is 15 cm.

moderate rains. Webs typically included a more or less dome-shaped sheet of relatively open mesh, with a sparse tangle of lines above which was more dense in the area above the top of the dome (Figs. 2, 3). The height of the tangle was generally between 0.5–1.0 times the maximum diameter of the sheet. The spider rested on the underside of the sheet at the peak of the dome. The dome was usually asymmetrical, with the peak near a large object (e.g., the trunk of a tree). The sheet on the side away from this object (the "exposed" side) was usually larger.

The dome was oriented more or less horizontally, so the peak was the uppermost part of the sheet (Figs. 1, 2). The exposed side was usually below the top of the dome, and its edge was often close to horizontal (Fig. 2). Orientations and shapes varied, however, with websites. For instance, some sheets were nearly planar (Fig. 4), while in other webs, built in small indentations in tree trunks, the exposed side of the sheet was nearly vertical (Fig. 5).

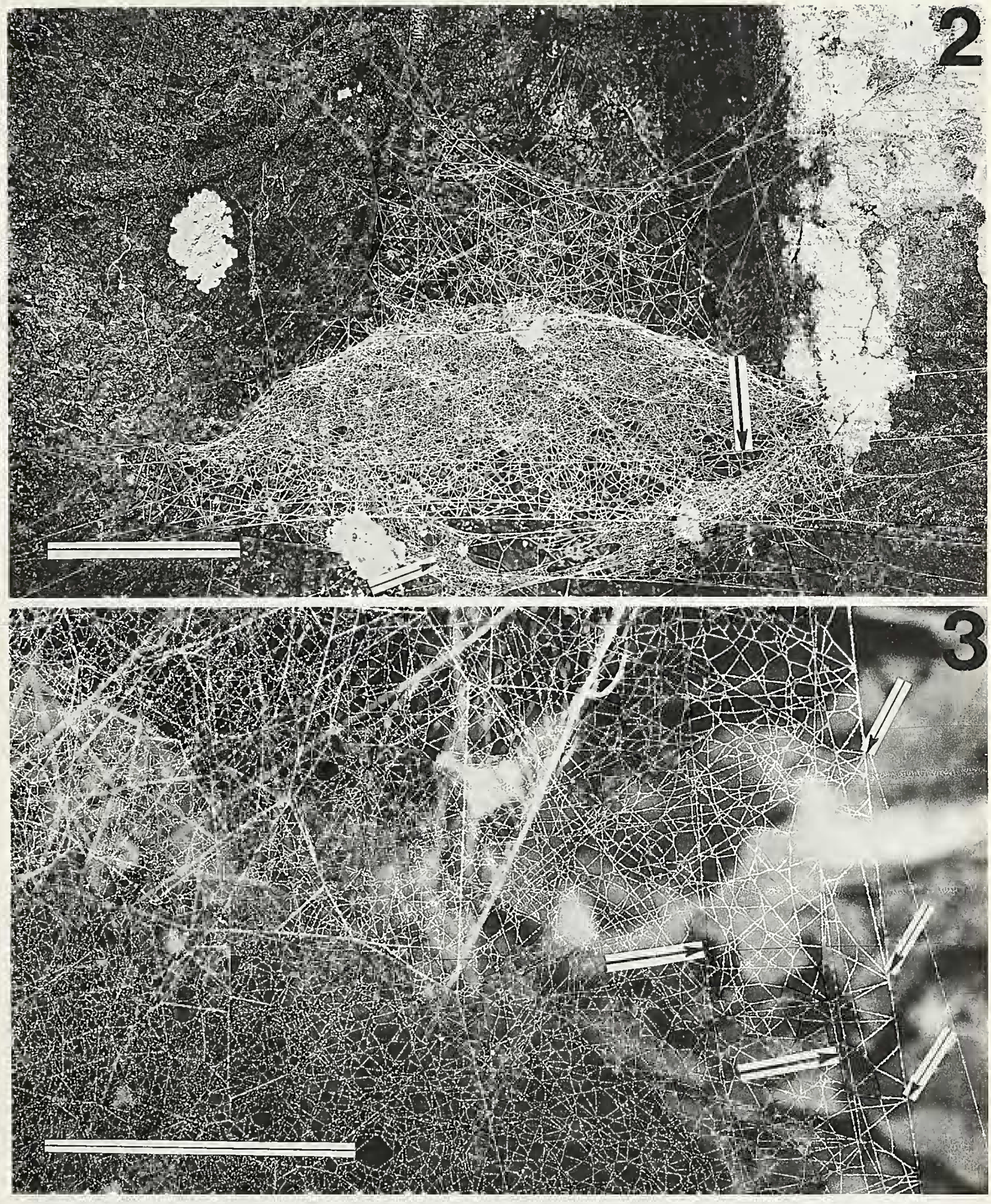
The lines in the sheet were not arranged in geometrically regular arrays, but they showed consistent patterns. Near the border of the exposed side, a few lines in the sheet were relatively straight (Figs. 2, 3); judging by the amount they sagged when coated with cornstarch, these lines were under more tension and/or were less extensible than the others. The lines forming the edges of the sheet were of this type. Other lines in the sheet which intersected the edges often had a "V" shape (Fig. 3). By powdering webs twice (see Methods), it was determined that the long, straight lines in the sheet were built during skeleton web construction, while the others were laid during sheet fill-in behavior (Fig. 6; see below). A further pattern, more marked in some webs than in others, was that the lines in the sheet near the exposed edge formed a more open mesh than those in the sheet near the peak of the dome (Figs. 2, 3, 5).

The size and shape of the web, as well as the density of lines in the sheet varied substantially between webs of the same individual. Replacement webs seemed to be smaller, with less densely meshed sheets (cf. Figs. 2 and 6), but no precise measurements were made.

Samples of three finished webs collected on microscope slides had lines of at least three different diameters. Many of the finest lines bore rows of small spheres. Near the exposed edge of the sheet these lines tended to run approximately perpendicular to the border of the web, which was formed by a relatively thick line. When a drop of water was placed on one sample, then allowed to evaporate, the spheres were reduced to small "ghosts", indicating that a major fraction of each sphere was water soluble. The junctions of thicker lines generally had masses of material that were probably attachment discs. In contrast, points where fine lines with balls crossed other lines generally lacked such masses.

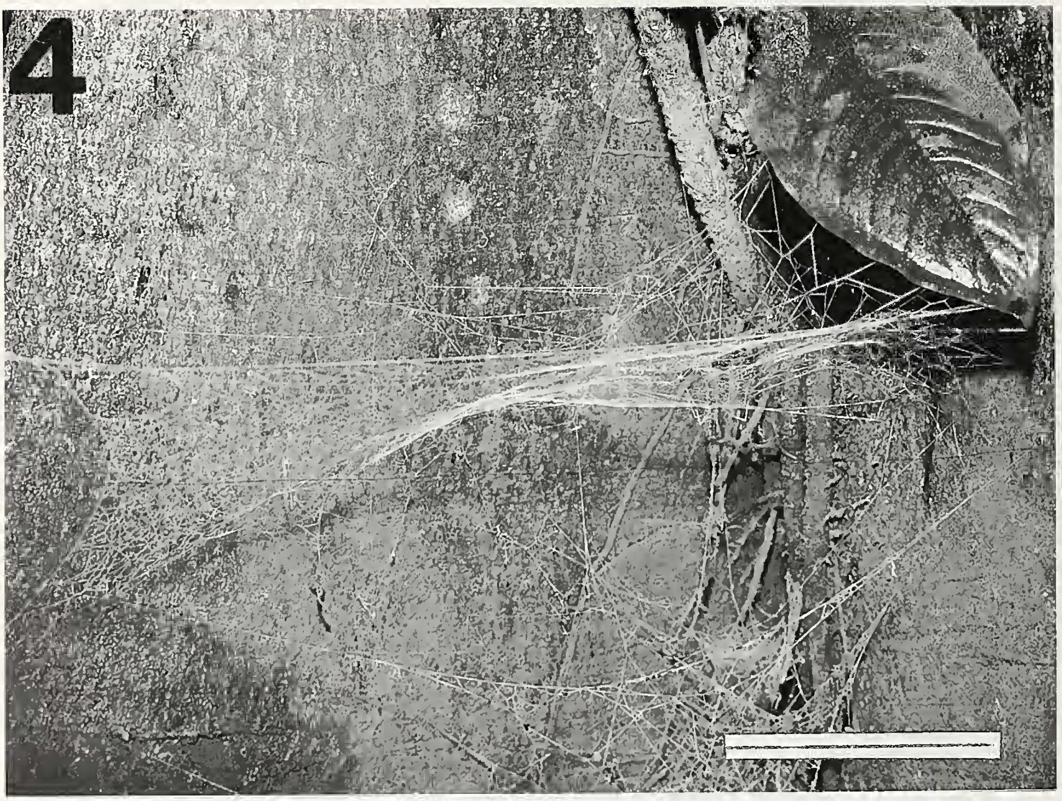
Construction behavior.—I distinguished three types of construction behavior: extending the skeleton web; filling in the skeleton web; and filling in the sheet. Construction always began with extension of the skeleton web, which was followed by alternating bouts of filling in the skeleton and further extension. A bout of filling in the skeleton was usually followed without a pause by filling in the sheet. This stage was less frequently interrupted by other activities, though occasionally a few attachments (probably filling in the skeleton) were made to the substrate and/or to web lines near a sheltered edge of the web. Sometimes the spider temporarily ceased filling in the sheet and rested at the top of the dome, only to resume this behavior 1–10 min later.

1. Extension of the skeleton web: The area encompassed by the web lines was gradually extended by additions along an edge. The spider



Figures 2–3.—A finished web of a mature female *Modisimus* sp. seen laterally (Fig. 2), and a closeup of the sheet on the exposed side of the web seen from above (Fig. 3). Heavy arrows mark relatively straight lines in the sheet, while others in Fig. 3 mark "V" junctions at the exposed edge of the web. Note also the remains of a previous sheet just below the new one (arrow), and the approximately horizontal edge of the exposed side (nearest the viewer) in Fig. 2. Scale bars are 3 cm (Fig. 2) and 2 cm (Fig. 3).

extended the web by first attaching its drag line one or more times to one or more lines already present, then walking to the end of the line on the web's edge and then along the substrate away from this web line (Fig. 7A). It usually moved more or less horizontally on the substrate. The spider attached its dragline to the substrate by bending its abdomen ventrally to touch the spin-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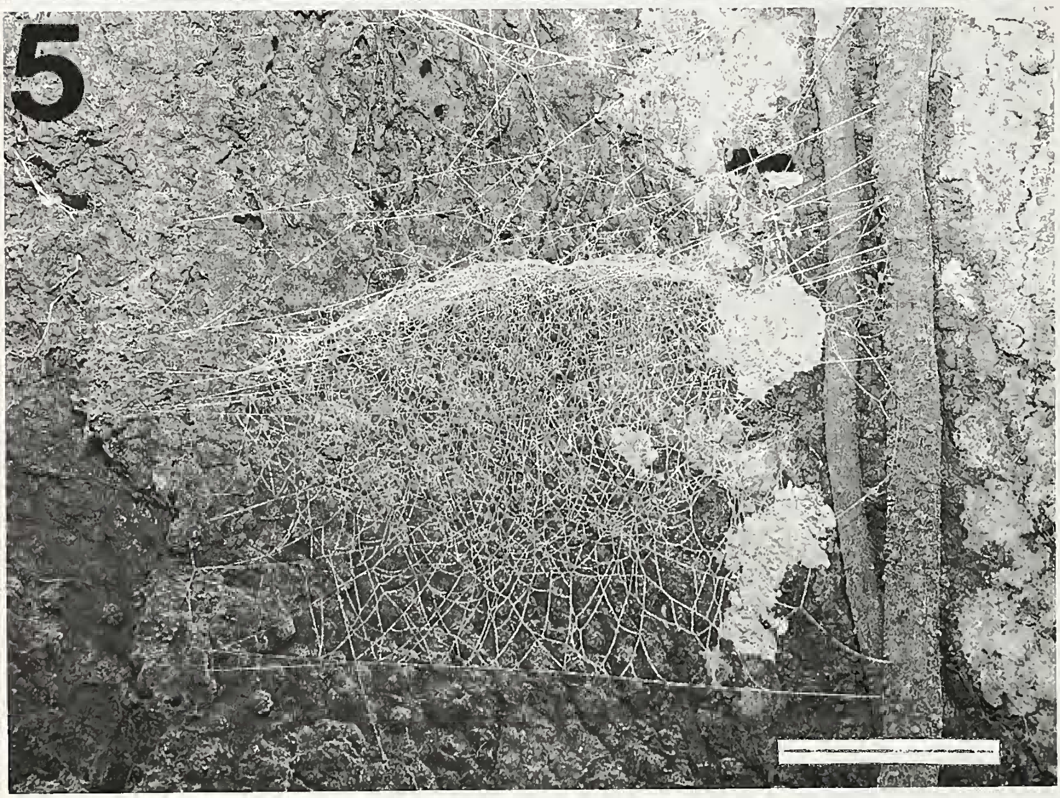
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Figure 6.—Lateral view of the web built to replace the web in Figs. 2 and 3 (note collapsed web against the tree trunk at right). The more heavily powdered lines of the replacement web formed the skeleton web that was built before the spider began to fill in the sheet. The lines laid as the sheet was filled in are more lightly powdered. Note the relatively long, straight lines of the skeleton web that are incorporated in the nearer, "exposed" portion of the sheet. Scale bar is 1 cm.

nerets to the substrate, holding the dragline with one extended leg IV as it did so (Fig. 7A). Then it returned along this newly laid line, attaching its dragline one or more times to it or to other web lines as it went (Fig. 7B). Often, especially soon after building began, the spider immediately went to the other side of the same edge of the web and extended it also in a similar manner (Fig. 7B). Occasionally the trip to the opposite side was abbreviated when the spider turned back before reaching the substrate and returned along the first side to extend it further. Up to six successive extensions on alternate sides of the same edge of the web were seen. A series of extensions usually ended when the spider attached its dragline part way across the border of the web, and turned to walk inward toward the area where the top of the dome would be located (Fig. 7C).

Early stages of extension of the skeleton web included lines laid above the plane where the sheet would eventually be in the finished web. In contrast, later extensions were always close to the plane of the sheet. Most extension occurred on the exposed edge of the web (e.g., side opposite the sheltering tree trunk). During web extension the spider seemed to walk more slowly than during later stages.

2. Filling in the skeleton web: After one or more web extensions, the spider moved around in the space encompassed by the web lines, attaching

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Figures 4–5.—Webs of *Modisimus* sp., illustrating variations on the basic domed form. The sheet of the web of a mature individual (Fig. 4) was nearly horizontal, rather than being domed. The sheet of the web of an immature individual was built in a small indentation in a tree trunk, and included a large, nearly vertical extension of the exposed edge (Fig. 5). Scale bars are 8 cm (Fig. 4) and 3 cm (Fig. 5).

its dragline to many of the lines it crossed. Each attachment was made by moving the abdomen ventrally toward the web line to which the dragline would be attached. At least one leg III grasped this line just anterior to the spinnerets. On some occasions the contralateral leg III also grasped the web line, also apparently just anterior to the attachment site. More rarely the IV leg ipsilateral to the III on the line also held the web line, in this case just posterior to the attachment site. In one case, a leg II also held the line just anterior to the leg III. I was unable to determine if any legs consistently held the dragline just before or during attachment. In some webs, but not others, the spider dropped down from the web at least once for 1–5 cm on a dragline, then ascended on the same line without having made an attachment.

Most filling in of the skeleton web was performed in the central area of the web, especially where the top of the dome of the finished sheet would be. Filling in of the skeleton web differed from web extension in that spiders were never seen to turn back after an attachment and walk along the line that had just been laid, even when this involved attachments to the substrate. In some cases, the spider did not fill in on the exposed side of the web in the area encompassed by the last several web extensions.

As during web extension, the spider consistently moved beneath lines already laid while filling in the skeleton, very seldom climbing up past a line to make an attachment (two exceptions were seen). As a result, the lines laid while filling in the skeleton tended to form bridges under the more upward projecting portions of the web which had been laid earlier (Fig. 8). Usually successive lines soon came to be concentrated in the plane where the sheet would be, but in some cases the lines did not form a plane at first, and the spider moved gradually lower, making a taller tangle of lines before finally forming a plane which would be the sheet. When I had only partially destroyed the previous web, the earliest skeleton web attachments were made to the very edge of the broken sheet, while later attachments were approximately 1 mm from the edge on the intact sheet. This resulted in the plane of the new sheet being slightly below the broken edge of the old sheet.

The combined processes of extension of the skeleton web and filling in the skeleton lasted 3–10 min. In the "completed" skeleton web (all the lines present when the spider began to fill in the sheet), the smallest mesh was where the top of the dome would be, often forming a small, nearly horizontal platform of relatively uniform mesh that was approximately the size of the spider as it rested on the web (Fig. 6). This area had a tangle of lines above it, and was surrounded by a more or less planar extension that was progressively less densely meshed farther away from this central area.

3. Filling in the sheet: The process of filling in the sheet usually took approximately 5–10 min. The spider walked in approximately straight lines beneath the skeleton sheet, repeatedly drawing silk from its spinnerets with its legs IV. The hind legs pulled the line (or lines?) and then pressed it upward against the sheet, where it stuck. The legs IV usually moved nearly synchronously upward, with one lagging slightly behind the other (Fig. 9). Occasionally they moved with alternate upward strokes, as described for similar behavior in other *Modisimus* spp. (Eberhard & Briceño 1985).

Lines laid as the sheet was filled in were occasionally attached by touching the spinnerets to web lines as described above. Such attachments were made almost exclusively to lines near the edge of the web, and were immediately followed by the spider abruptly moving toward the central area, thus producing a "V" configuration of the sheet fill in lines (e.g., Fig. 3). No attachments were made to most other web lines encountered as the sheet was filled in. In one case, with fa-

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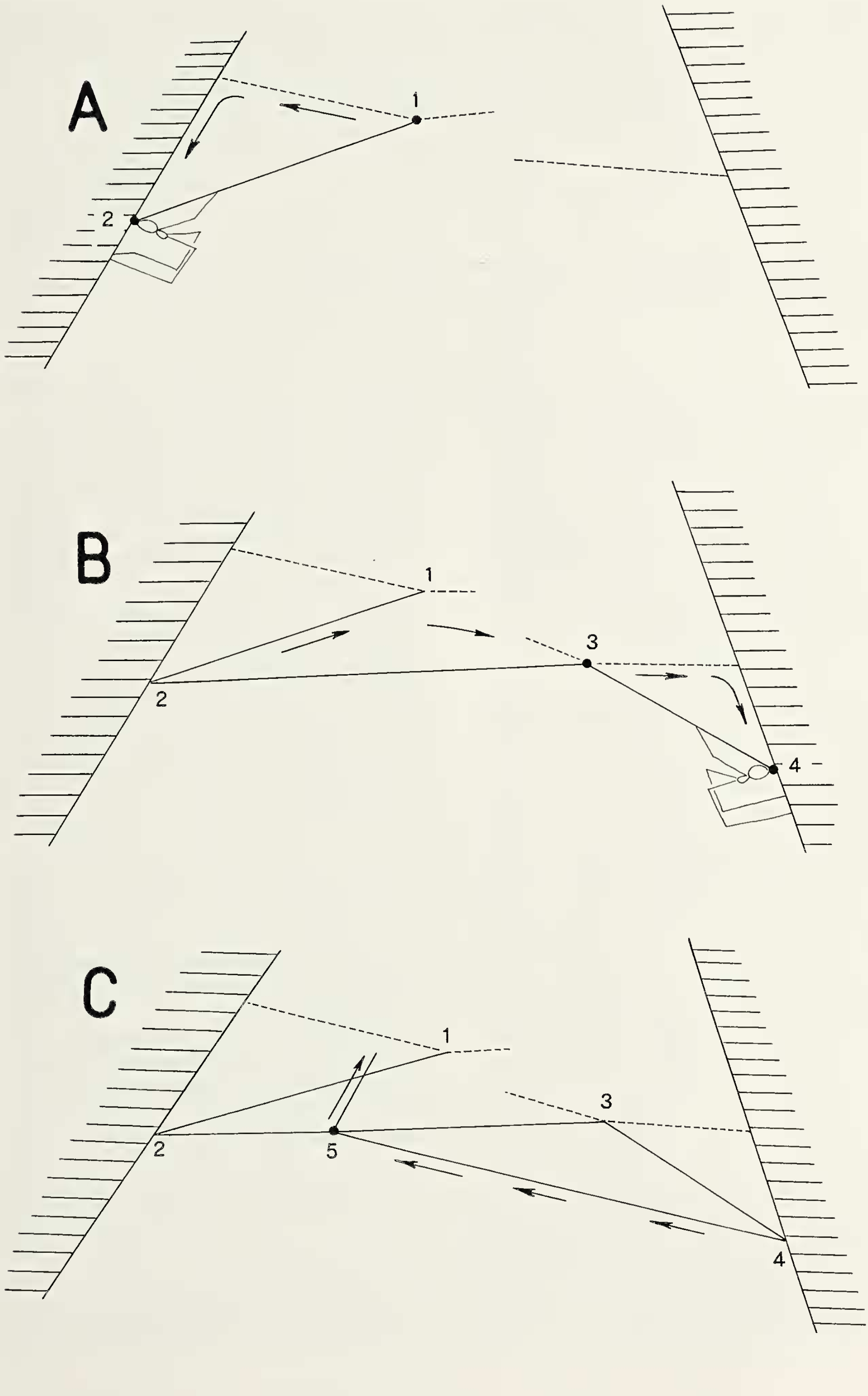
Figure 7A–C.—Schematic representation of two successive typical web extensions, seen from above. Lines present before the web extension began are dotted, and attachments made during each figure are dots. Numbers indicate the sequence of dragline attachments. **A**. The spider attached its dragline to a line at the edge of the web (1), walked to the substrate along a line, and then walked away from this line before attaching its dragline to the substrate (2). **B**. The spider returned along this newly laid line to the edge of the web and attached there (3), then walked farther along this edge to the substrate on the other side and attached there beyond the previous edge of the web (4). **C**. The spider returned along this newly laid line, attached its dragline part way across the new edge of the web (5), and moved toward the interior of the web.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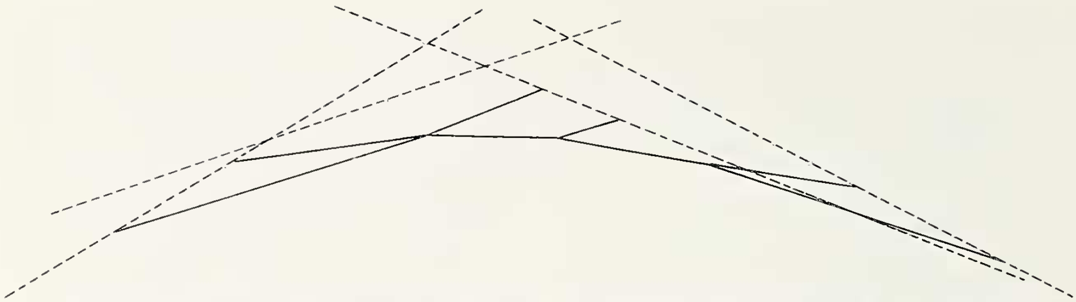

Figure 8.—Lateral schematic representation of how the lower portion of the skeleton web was lowered and smoothed as the spider attached lines exclusively on the underside of the web as the skeleton web was filled in. Lines laid early are dotted, those laid later are solid.

vorable lighting in which the skeleton web lines had been powdered, I noted that lines laid as the sheet was filled in were not tense, and moved slightly in very weak air currents.

I collected samples of two webs on microscope slides just after the spider began to fill in the sheet, and found that the fine lines with balls on them that were common in finished webs were nearly completely absent. Thus these presumably sticky lines were added to the skeleton web when the sheet was filled in.

DISCUSSION

There seems to be a simple organizing "principle" at work during web construction by *Modisimus*, in both the horizontal (Fig. 7) and the vertical (Fig. 8) dimensions. The spider first extends the sides of the angle formed by the limits of the web (e.g., Fig. 7A), then fills in the space between the new sides with further lines (e.g., Fig. 7B, C). In the horizontal dimension this process occurs repeatedly, and involves new attachments to the substrate. This enables the spider to extend the web in accord with the open space available. The spiders' long legs permit them to span relatively large spaces, and thus move easily across irregularities in the substrate.

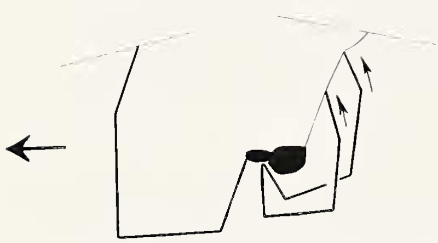

Figure 9.—Diagrammatic representation of movements made as the spider filled in the sheet. The spider moved across the underside of the skeleton web (horizontal arrow), pulling a line or lines from its spinnerets with its hind legs and pushing upward (vertical arrows) against the web. All legs other than one leg I and the two legs IV are omitted for clarity.

In order to perform horizontal web extensions effectively, the spider must take into account which side of the web already has lines present when it turns after reaching the previous attachment to the substrate (e.g., turn to its left in Fig. 7A). This is necessary if the spider is to extend the web by laying its new line on the side of the previous attachment which lacks lines, rather than add another line to the area already covered. Spiders seemed to make such distinctions quite consistently, as I never saw a spider walk to the leading edge of a web, then walk in the wrong direction along the substrate and attach a line and return to the web along it. Possibly this discrimination was accomplished by having some legs holding web lines other than the line along which the spider moved out toward the periphery. Memory of distances and directions travelled (an apparently ancient and widespread capability in arachnids; see Eberhard 1988) may also be involved.

In order for the lines and attachments which are laid after a web extension attachment to the substrate to extend the web, the spider must return along the line it has just attached to the substrate, rather than along previously laid lines. This may explain why spiders consistently held the dragline with one leg IV as the attachment to the substrate was made (Fig. 7). In contrast with many orb weavers (e.g., Eberhard 1982), *Modisimus* sp. frequently failed to hold the dragline in other situations.

The web construction behavior of *Modisimus.* sp. and that of two other *Modisimus* species

(Eberhard & Briceño 1985), which also build domed sheets with small tangles above, are probably very similar. All three species began construction by laying a scaffold of thicker lines without sticky balls on them. The first two stages of construction behavior described here (extension and skeleton fill in) apparently correspond to the "Phase I" of the other two *Modisimus* spp. (Eberhard & Briceño 1985). These species also have long, straight lines near the edge of the sheet. The later stages of construction by all three species consists of filling in the plane of the sheet, using legs IV to pull out lines and then push them against the sheet. Lines laid at this stage carry sticky balls (Briceño 1985) in at least two of the species. In all three species, attachments of both lines in the skeleton web and of sheet fill in lines to the edges of the skeleton web are consistently made while one leg III holds the line to which the attachment is being made just anterior to the attachment site. Similar use of one leg III during attachment of the dragline also occurs in the pholcid *Physocyclus globosus* (Eberhard, unpubl.).

The establishment of a sparse network of lines followed by the addition of interconnecting lines in *Modisimus* sp. also resembles the construction process described for some theridiid spiders (Lamoral 1968). The pholcid differs, however, in establishing the first lines in non-radial rather than radial directions (e.g. compare Fig. 7 with fig. 7 of Lamoral 1968), and also in having a much tighter mesh away from the edge of the skeleton web.

Pholcids are thought to be only very distantly related to orb weavers (Lehtinen 1967; Shear 1986). A comparison of the organization of the webs and web building behavior of *Modisimus*. sp. with that of orb weavers suggests three basic similarities. First, in both web types a scaffolding of non-sticky lines is built first, and used to sustain sticky lines laid later. Second, in both web types the outlines of the scaffold are built first, and then gradually filled in, first with other non-sticky lines (although in the pholcid these two stages were more often mixed together), and then with sticky lines. Finally, construction of both web types is clearly organized around a central area (the hub of an orb, the peak of the dome of the pholcid web).

These presumably independently derived similarities support the view that some orb-associated traits, such as construction behavior that is organized in a plane around a central area, and construction of a non-sticky scaffold which is then filled in with sticky lines, are not limited to orb weavers (Eberhard 1990a). However, in the pholcid web the lines do not radiate from a central area, as do the radii of an orb, and neither sticky nor non-sticky lines are organized in circular or spiral patterns. Thus the behavioral similarities are not reflected in the geometric patterns of lines in the finished webs.

Another difference is that the pholcids did not break lines and reconnect them during web construction. The early "exploration" stage typical of orb web construction seemed to be absent, except for occasional descents without attachments, which resembled similar descents of some orb weavers (Eberhard 1990b). All other lines laid from the start of construction were included in the finished pholcid web. Probably this lack of line replacement behavior is a primitive trait. The absence of line removal was not due to the pholcid being unable to cut lines, as on several occasions during skeleton web construction a spider neatly cut out a piece of debris and dropped it free. In no case, however, did a spider break a line, then attach its dragline to one broken end and reel up the other as it walked on, as occurs in many orb weavers (Eberhard 1982, 1990b; Coddington 1986a,b; Shinkai 1990) as well as in some theridiids (Szlep 1966; Eberhard in press b).

Perhaps *Modisimus*. sp. cannot effectively remove lines already laid, and must correct early mistakes in skeleton web construction by adding subsequent short lines which change the outline of the lower margin of the mesh which is being formed, in effect replacing the earlier lines by lowering the site where the sheet will be made. This implies that at least some of the tangle above the sheet may represent exploration behavior. However, I was unable to discard the alternative possibility that differences in the height and numbers of lines in tangles represented adjustments to particular website characteristics.

Several other pholcids make more or less domed sheets (*Blechroscelis* sp. and *Modisimus* spp.–Eberhard & Briceño 1985; *Physocyclus globosus*–Eberhard in press a). More or less domed sheets also occur in several other families such as Diguetidae (Nuessly & Goeden 1984), Theridiidae (Main 1976; Shinkai 1984), Hypochilidae (Shear 1969), Linyphiidae (Nielsen 1931; Kaston 1948), and Araneidae (Kullmann 1964; Shinkai 1984). The functional significance of the domed form is not clear. Domed sheets might be designed to capture prey which is flying upward, as a dome could work in a manner analogous to a malaise trap, using the prey's tendency to fly upward to channel it toward the spider. However, *Modisimus*. sp. often built new webs just above the remains of previous sheets (Fig. 2). These old webs would make it difficult for prey to reach the new web from below, and thus argue against the malaise trap interpretation, at least for this species.

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